V. *The Egg-laying of* Trichiosoma (Tenthredinidae). By T. A. Chapman, M.D., F.Z.S.

[Read February 4th, 1914.]

Plates X–XVI.

In the Presidential Address to the Entomological Society on January 12, 1912, by the Rev. F. D. Morice, we have a résumé and critical estimate of all that was known up to that date concerning the action of the ovipositors (saw, terebrae) of the sawflies (*Chalastogastra*), together with some very careful and important observations by Mr. Morice himself on one species of the group.

This Address stimulated my interest in the operation of oviposition in the sawflies, which I had often wished to observe, but had never succeeded in actually seeing.

It curiously happened that in the spring of 1913 an extremely favourable opportunity of doing so occurred to me, and the details observed seem to be worth relating, because they were so very clearly seen, and for another circumstance which appeared as a result, viz. that they differ to some extent in the different species (or genera ?) of sawflies, and that consequently my observations are not merely a confirmation of Mr. Morice's report, but rather an extension in a new direction.

It was on the 22nd April, 1913, that I saw in the marshes at Reazzino, near Locarno, a specimen of *Trichiosoma betuleti* (?) in the act of laying an egg in a leaf of a small smooth round-leaved sallow. I watched it lay a second egg, but not having a lens did not see much of the process. On the way home I found another specimen of the same species at rest on a poplar trunk. A good many searches on later occasions failed to result in the discovery of any further specimens. These two flies I took home and kept in captivity for two or three weeks.

I was very much struck by their quiet sluggish behaviour and by the fact that during the whole time I had them, neither of them made any attempt to use her wings.

I think it is probable that both had already laid the majority of their eggs, as they were rather hollow in appearance and only laid a dozen or so eggs each for my benefit.

I only gave them access to material on which to lay, when I was at liberty to observe them, so that I was able to follow the whole operation in the case of every egg that was laid.

I fed them occasionally on water, neither sugar nor sap expressed from the sallow seemed to tempt them. They took the water freely but with extreme slowness, as if it had to be absorbed rather than swallowed. This was accompanied by what might be called chewing movements of the maxillae, labium and palpi. The centre of the mouth parts could not be well seen during the sucking process, but seemed to have a bag-like appearance.

What made the examination of the whole process of egg-laying so easy to observe, and therefore (comparatively) so easy to understand, depended on the large size of the insect, on its very placid nature so that when laying it could be moved into any position and approached as closely as necessary with a lens, without in any way disconcerting it. It was further facilitated by the circumstance that the most satisfactory way of looking at the process, viz. in profile, was also the most obvious and easiest. The upper cuticle of the leaves, beneath which the pouch for the egg is made, is perfectly transparent and the rest of the leaf quite translucent.

The sallow on which I found the *Trichiosoma* laying belonged to the *Caprea* group, but I do not know its name; it had a somewhat regular oval leaf, rather small, and in the young state in which the eggs were laid it is quite glabrous. This last seemed an important character to the instinct of our sawfly. Having difficulty in getting the desired sallow, I tried the flies with other species of *Salix*, but they refused all I tried except one that seemed to me to have nothing in common with the original sallow, except that its leaves were glabrous; this was a willow, possibly *Salix fragilis*, grown in the vineyards at Locarno, for training the vines on and for supplying withes for tying them. In describing the leaves of these two species as glabrous, I am not strictly accurate, they were glabrous compared with other available species of *Salix*, and really seemed so when only the immature leaves that suited the *Trichiosoma* were uncritically observed, but they actually had some hardly visible hairs that were more obvious when the leaves matured.

The leaves selected by the flies were those that were

nearly but not quite fully expanded and had very delicate tissues, younger leaves were several times accepted but never older ones.

Poplars margined the wayside where I found the insects, and as the quality of its leaves is very similar to that of the *Salices* affected, I think it not improbable that the poplar is also patronised.

The subject of this paper is the action of the saws, so that the precise determination of the species of *Trichiosoma* observed is of less importance. This is fortunate, as Mr. Morice does not find it easy to say which species is in question; for my purpose it will be enough to report that he says, "I should feel quite certain that it was *betuleti*, Kl., if only you had not found it on *Salix*—" "—*betuleti* has always been believed to be exclusively attached to *Betula* and—mainly on that account—has long been reckoned as a variety of the well-known and universally distributed *T. lucorum*, which abounds wherever *Betula* is plentiful. The only two species recorded as attached to *Salix* are *latreillii* and *sylvatica*; yours, I am satisfied, can be neither of these, unless all Trichiosomas are forms of a single species."

He adds that the species is almost certainly the *betuleti* of Costa, which is placed by Cameron under *lucorum*, and is not the species given as *betuleti*, Kl., by Cameron ("British Phytoph. Hymenoptera," Ray Soc. Vol. III, pp. 22–24).

I have various notes made at the time, some of which I may quote. I also made some rough diagrams of the progress of the operation of cutting the pockets, etc. These I elaborate a little, but they still remain only diagrams; I am no draughtsman, but if I were, the operation, though slow enough for observation, is much too rapid for any careful drawing.

On April 26, I note that I saw "5 eggs laid on the smooth narrow-leaved willow. The sawfly crawled about in a haphazard sort of way, much as when moving with no obvious object. Almost unexpectedly, however, she would come to a spot with the end of the abdomen against the margin of the leaf, and there resting, a rhythmical movement of the end of the abdomen took place; at first this seems to be a process of the two larger front eminences endeavouring to get a hold of the margin of the leaf or some sort of fixity in regard to it, so that the saws could properly begin to operate."

These "eminences" I take to be what Mr. Morice calls "the apical plates of the saw sheath," they remind me in position and structure of the 10th abdominal segment of many female Lepidoptera, a pair of rounded plates, well clothed with hairs, not densely, but spread and especially marginal, and impressed one that they were for precisely the same office as the very important one in the Lepidopterous structure, viz. to verify that the situation selected, and in fact to select it, is exactly what is required, in the one case for laying the egg, in the case of the sawfly, for cutting the pocket.

The insect is resting on the leaf with legs on both sides of it, and with this fulcrum is able to press the abdomen sufficiently against the leaf. The two apical plates do not grip the leaf, but still, with its margin actually or apparently between them, give the selected place the required steadiness. The one facing the observer covers the actual point of entry of the saws, but the movements noted above are really the beginning of their operation and their actual entry into the leaf. They do so "on the upper surface, but so close to the margin that I am not quite positive that the actual margin is not the real or intended place. When the operation is finished it is practically impossible to verify any actual opening, but one guessed it to be some 0·1 mm. from the margin on the upper surface. The body of the insect is so placed that the plane of the leaf coincides with the median antero-posterior plane of the insect." Fuller observations on more specimens of the work, shows that the incision is on the upper surface, parallel with the margin and nearer 0·3 mm. from it than the distance noted above. "When once the saw enters it works very rapidly and the full extent of cutting is done in from about a minute to a minute and a half. This is guessed, as I was too intent on observing the process to note the watch at the same time; but in one instance, I found that there was a rest of 10 seconds at the end of the cutting, and that the laying of the eggs and extraction of the saw took place in 15 seconds. In observing the action of the saw, two circumstances made this much more satisfactory than I had anticipated. One was the absolute transparency of the upper cuticle of the leaf, beneath which the saw penetrated, the parenchyma of the leaf being below the saw; the other was that during part of the operation, a portion of the saw between the leaf and the body of the

insect was free, so that taking the insect in profile, the whole process was very easily seen, the saw within the leaf being but little obscured by the translucent leaf substance below it cutting off the light. Nothing, however, could be seen from the lower side of the leaf owing to the thickness of the leaf substance between, which, though translucent, was by no means transparent."

"When the saw is first seen to have really entered the leaf, the darker posterior (in the then position of things) portions of the saw (the 'supports') advance slowly, steadily and uniformly together; whilst the anterior members (the 'saws') are seen to be in rapid motion."

To understand the method of this movement, it is necessary to remember the structure of the whole terebra. This, as it exists in *Trichiosoma*, is shown in the photograph on Plate XV, and in figs. 11 and 12 of Plate XVI.

Mr. Morice calls attention to the fact that these terebrae present in different species, different relative developments of the "saws" and "supports," no doubt in accordance with slightly different methods of operation according to the requirements of each species in regard to the material in which the eggs are laid and their disposition therein. The justification for my recording my observations is that in *Trichiosoma* the details of structure and procedure do differ from those observed by Mr. Morice in *Phymatocera aterrima*, Kl. In that species both saws and supports terminate together in what forms an acute point to the terebra, which apparently makes its first entry by a process of stabbing. In *Trichiosoma* there are no sharp points, the saws continue round the ends of the support, so that the end of the terebra is not a point, but a continuation of the cutting edge of the "saws," which even go round the support so far that the cutting edge at their tips faces in a posterior rather than an anterior direction.

Mr. Morice tells us that these terebrae are not merely objects in two dimensions but in three, and have a thickness that in some species probably enables them to act more or less as wedges. Though an object of two dimensions only is a mere mathematical abstraction, nevertheless in *Trichiosoma* the whole cutting action takes place in such a way that we need not take into account that it has any thickness, it is indeed so thin that one almost wonders how it can possess the necessary strength. Each saw and support has indeed a structure much like that of a

lattice girder, so as to secure much stiffness, and any buckling is prevented by the instrument being confined beneath the leaf cuticle at the time when it is subjected to the greatest strains.

The saw "is curled right round the end of the guide (support) and goes to and fro rapidly, without however altering its position. At first glance the movement is rather a twinkling than a to-and-fro movement, but it is soon realised that, the saw being double, one portion advances as the other retreats. This is easily seen in the portion between the leaf and the insect, where there is nothing either in front or behind the saw.

"The cutting is done by the margins of these two pieces at the end, and advancement is rapid, steady and uniform, but the actual alternating movement of the saws across the line of advance is much more rapid than the actual advance, perhaps four or five times as rapid."

The penetration of the leaf is first directly inwards from the edge, and during this period the cutting is done by the portions of the saws that curl round the end of the supports. When the terebra is engaged to its full length directly inwards, it has cut a space under the cuticle just sufficient to hold it, or wider by the trifling amount that the saw curls round to the other side of the support. The twinkling continues but the cutting is now done forwards by the front margins of the saws, and continues doing so till the terebra swinging forward is about parallel to the edge of the leaf, with its extremity in the same direction as the insect's head, and has behind it a free space or pocket approximately circular. "When this position is reached a short rest takes place, then, after some 10 seconds or so, some movements hardly affecting the terebra, but of a similar but rather slower and more heaving character than when cutting is being done, take place more in the body of the insect than in the terebra. This is hardly noticed before the egg begins to occupy the saw, which resumes movements similar to those used in cutting and which probably assist the advance of the egg between its right and left portions, which must now be separated enough to admit of its passage, though the distension is too slight to be observable. "The actual egg when laid is a fairly large and thick oval body that occupies practically the whole pocket. In the actual laying the appearances seem to compel one to believe that in its

passage the egg is drawn out into a long spindle shape. The egg gradually appears at the anterior margin of the saw, the saw working as during cutting, not at its base but along its whole length, and whilst the saw is still in the position in which it stopped cutting. Gradually the egg grows larger and, in doing so, the saw passes back into the lower portion of the space cut, apparently pushed by the increasing egg, and when the saw is quite pushed back the whole egg is seen to be present and the saw (terebra) is in a second or two withdrawn. At the first appearance of the egg only a narrow margin is occupied by the portion present, and one can only suppose that the shell is sufficiently extensible for the rest of it to be in the basal portion of the saw and the body of the insect." When half laid it must have quite a dumbbell shape, one rounded end in the pocket, the other within the body of the insect, the narrow connecting portion in the neck of the terebra.

It may be observed here that in *Phymatocera* the terebra was withdrawn after the pocket was cut and replaced to lay the egg, but in *Trichiosoma* no such break occurred, only a short rest being taken with the terebra still *in sitû*.

Mr. Morice, indeed, relates that the process of rotation towards the body of the insect, apparently precisely like that in *Trichiosoma*, was not as in *Trichiosoma* stayed when a pocket was formed, but continued until the terebra cut its way out, and in the result, the process being repeated, there was a long clean cut or slit with a succession of eggs, laid along it. In *Trichiosoma*, the original incision of entry is never enlarged, and each egg is laid in a separate and independent pocket.

"On one occasion the saw came to a vein in the leaf, which it seemed to find to be an impediment and it was at once withdrawn. On another occasion the pocket was all but finished, but the original line of entry seemed to have been too oblique, with the result that the forward movement of the saw brought it to the margin of the leaf before the pocket was quite large enough, though to my eye it was very close to full size. This was not, however, satisfactory, and the saw was withdrawn without any egg being laid."

"April 27th. Sawfly quite refused to experiment with a slightly rough hairy-leaved willow. Saw two eggs laid to-day on smooth willow. Timed one of these. From the fly settling down to the saw actually entering forty seconds (40″), from this to completion of the straight entry,

one minute (60″); to the completion of cutting, further fifty seconds (50″). Then ten seconds (10″) rest, and in fifteen seconds (15″) more, the egg was laid and the saw withdrawn."

On this occasion by giving attention to the point it was clearly seen that the points of the saw curled round far enough to cut a narrow portion behind the guide.

I ought to have noted that in captivity at least it seemed quite immaterial to the flies whether their heads when laying were directed towards the tip or the base of the leaf, nor did I notice that the legs were disposed in any constant manner to secure a correct foothold.

On May 1st the two Trichiosomas were getting rather exhausted (they had probably been in existence some time when captured). One could not be got to lay; the other laid two eggs, but was rather stupid about it, as though her instincts were failing. She kept getting too much on the face of the leaf instead of on the edge, so that on three attempts she failed to penetrate the leaf, the end of the saw being too vertical to the face of the leaf and not in the same plane with it, though I would not be positive that she did not penetrate the cuticle but could then go no further. On the two successful occasions, either from being out of proper alignment or simply from exhaustion, after taking about a usual time, 1′ 20″, to pierce, and 1′ 0″ to traverse, she then rested in one case 3′ 0″ and in the other 4′ 0″ instead of the usual 10″ or 15″, the actual laying and withdrawing being as usual. Certainly the day was dull and cool; for a successful observation a fairly warm day and suitable fresh *Salix* were always necessary.

The eggs were laid in leaves on cut branches in water, so that their not increasing in size may be their usual habit, or may have been the result of a want of a natural flow of sap in the plant. The eggs I have had of several species of sawflies have expanded in this way very notably. I fancy, however, this species does not do so, as the egg duly hatched in an apparently normal manner. On May 1st, eggs laid on April 22nd had shown for several days the outlines of the contained larva, as a denser circle within the margin, but all very translucent and free from visible structure except one small brown spot; at this date the spot had got larger and more distinct, and had a rhythmical to-and-fro movement, approaching and receding, by a small distance, the end of the egg nearest the inlet to the

pouch (micropylar end?). The movement occurred to and fro twenty times in a minute in one case in which I counted it. In another egg it is slower and in a younger egg, in which the spot is not so well developed, it occurred only at considerable intervals. On investigation it appeared that the brown spot is one of the eyes of the larva, quite distinct, being only under the transparent cuticle of the leaf; the other is invisible, being on the other side of the head and can only be glimpsed from below, owing to the thickness of the parenchyma of the leaf. The movement is really a periodical rotation of the head of the larva.

The movement in the earliest (April 22nd) eggs ceased on May 3rd, and on May 4th the first larva hatched. The young larva is very large for the size of the egg, 7 mm. long, green, with large brown (or black) eyes and a dark spot in the middle of the labrum. It escapes by an irregular tear in the thin cuticle, sometimes of considerable length, sometimes small, so that it seems the larva could hardly have got through it.

On the 14th of May the larvae had moulted to 2nd instar, the largest 15 mm. long, but not yet full-grown in that instar. They are pale, almost colourless, except for intestinal contents. They become rather white and opaque, and the interior obscured, by an efflorescence, which is not present just after moult and easily rubs off. Except for size these larvae were very like those one is familiar with on hawthorn. Exigencies of travel led to their being so ill used that several reached the 3rd instar, but none got any further.

The egg all but fills up the pouch and measures 2·5 mm. parallel with the length of the leaf and 2·0 mm. across, the branch of the pouch towards the opening seems to get more or less glued together and is sometimes quite visible, in other cases cannot be made out.

In carefully watching with a good lens the laying of some two dozen eggs, the question present to me was always how is the cutting actually done, is it cutting, carving, tearing or what? I concluded that it was none of these, but really the action of scissors, something like the action of a reaping- or mowing-machine, or even more closely of horse-clippers. Each of the projections of one of the "saws" in passing a similar projection of the other acted with it as a pair of scissors cutting through the scrap of tissue caught between them. In making the pocket, *i. e.*

in separating the layer of cuticle, what has to be cut through is the vertical walls of the cells of the leaf, which being only the divisions between the cells, have much less area than the whole of the pocket, and being very thin and (in these young leaves) very soft and tender, are easily caught between the projecting blades of the saws and cut through. The actual beginning of the process, the entrance of the terebra into the leaf, was always obscured by the portion of the sheath referred to already. It always took a time greater in proportion, one felt, than the cutting of the pocket afterwards. This resulted, no doubt, from the fact that cutting had here to take place over the whole line of advance and not merely at the widely separated dissepiments of the leaf cells. The flies would only use young and tender (in fact, not fully grown) leaves, and whilst this would facilitate the cutting at all stages of the process, it would be important at the first penetration, as the saws could not cut unless the cuticular tissue was soft enough for them in some degree to indent it. This advantage or necessity would of course be much the same whatever the precise manner of cutting was. The analogy or rather identity with scissor action, or multiple scissor action as in horse-clippers, is perhaps more easily realised when it is called to mind that the two saws are strengthened lattice-girder fashion by transverse thickenings on their outer surfaces, which are thus uneven and irregular, but that their opposed faces are quite flat, sliding smoothly on each other precisely as is the case with the opposed faces of scissors or clippers.

Mr. Morice has added to my indebtedness to him in the matter of this *Trichiosoma* and its correct position as a species, by giving me the photographs on a much enlarged scale of the extremity of the terebra, and still more enlarged of its cutting edge, which are reproduced on Pl. XII.

Explanation of Plates X—XVI.

Plate X shows *Trichiosoma* in its relative position to the leaf when ovipositing. Photograph from a specimen mounted on a leaf that had an egg laid in it. The pocket from which the larva duly hatched is seen on left, opposite end of wing. The terebra is in

about the position it occupies when the direct penetration is nearly completed, but *on* the leaf instead of in it. Magnified × 3.

The photographs on Pl. XI show the terebra of one of my actual flies × 25. I have found it impossible to mount for photography the terebra with the two blades in natural opposition. Here they are somewhat slid apart, with this advantage, as it happens, that the two saws are not advanced to precisely the same place in each : in one it is fully advanced, in the other somewhat withdrawn, and their actual movement in cutting is alternately from one position to the other, the one advancing as the other retreats. The other photograph, from a specimen not taken by me, shows the terebra separated into its four constituents, two guides or supports and two saws—a condition to which they are only too easily reduced in mounting.

Plate XII shows the further enlargements of the extremity and margin of the terebra, for which I am indebted to Mr. Morice.

It seemed desirable in order that my notes should be capable of being easily understood that I should present some figures. For this purpose, I have in some degree improved the diagrams I made at the time, but they remain only crude diagrams, useful, I hope, to give greater clearness to my descriptions of what I saw, but not to be in any way trusted outside this object.* In the first place I wish to describe movement; this is, of course, quite absent from the diagrams. But, further, to make them simple, I have used a photograph of one blade only of the terebra. In the absence of movement, this is unimportant; some day, perhaps, some one may secure a cinematographic film of the whole operation.

The diagrams are magnified about 18 diameters.

Pl. XIII, figs. 1, 2, 3, and 4, attempt to show the progress of the terebra into the substance of the leaf immediately below the upper cuticle and practically at right angles to the margin of the leaf. The whole incision so made is just so much wider than the width of the terebra, as the tip of the saw curls round the end of the guide and so cuts a fraction beyond its margin.

Direct movement into the leaf ceasing, the terebra then moves forward as shown in

Fig. 5, until it reaches the position shown in

Fig. 6, when the pocket is completed. After a short rest the laying of the eggs begins.

Pl. XIV, fig. 7. At this early stage a strip of the margin of the egg

* For example I show the pocket, so far as cut, as a blank, but, in fact, the cuticle returns to its position, and the appearance is almost the same when the pouch is formed as it was before.

appears to be laid, but as by no conjuring can the rest of the egg be between the plates of the terebra, it is evident that the egg has now no spherical form, but that the rest of it is within the body of the insect, and at this stage and the further one shown in

Fig. 8, the egg is seen to stretch along the terebra as far as the transparency of the parts allow, up to the thick opaque sheath of the terebra; in fact, into the body of the insect. In Pl. XV.—

Fig. 9, though much of the egg is within the pocket, a portion still connects this portion with some still within the insect. During all this time the egg must be in a very soft plastic condition, so as to be capable of being stretched out and moulded to suit the necessities of the position.

Fig. 10 shows the egg nearly all laid. As the laying is completed so the terebra descends to quite the bottom of the pocket, and with hardly any interval is withdrawn.

Pl. XVI, fig. 11 is the egg some time later (still quite diagrammatically) to show the positions taken up by the eye of the larva. Only one eye is seen, but this moves rhythmically between the two positions shown in the diagram.

Fig. 12 is a pocket after the larva has escaped (this under camera), showing the rupture by which the larva emerges, in this instance decidedly smaller than usual. This diagram is on a slightly larger scale than the others.